# A HERBACEOUS LYCOPHYTE FROM THE LOWER CARBONIFEROUS DRYBROOK SANDSTONE OF THE FOREST OF DEAN, GLOUCESTERSHIRE

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ABSTRACT. Leafy lycophyte shoots preserved as impressions and as material resembling fusain are described from a shale band in the Drybrook sandstone (Upper Visean), Puddlebrook, Forest of Dean. The consistently narrow stems with small terminal strobili bearing megaspore impressions place this material in *Selaginellites* Zeiller (1906). Fusainized material shows fine surface morphology and anatomy of the leaves and stem. The large number of specimens demonstrates a wide range of morphological variation in the position and shape of attached leaves. In particular, the impressions and fusainized preservation of laterally attached microphylls, which are orientated perpendicularly to the bedding plane, are often drastically altered from their original laminate structure. The leafy shoots show some similarity to those of *Clwydia decussata* Lacey (1962) and *Archaeosigillaria kidstonii* Kräusel and Weyland (1949). These plants are also discussed in the light of recent approaches towards the interpretation of lycophyte impressions and compressions. The new material is assigned to *S. resimus* sp. nov.

ONE of the major difficulties in reconstructing fossil lycophytes from compression assemblages is the inevitable fragmentary nature of the material and the problem in identifying specific characters common to large axes and the much smaller leafy shoots. A situation, therefore, may exist where narrow lycophyte axes from a given assemblage could represent either a herbaceous element or the unattached distal parts of an arborescent organism. For this reason relatively few truly herbaceous lycophytes are known from Carboniferous compression floras in spite of the abundance of small lycophyte shoots (Thomas 1967; Chaloner and Collinson 1975; Chaloner and Meyer-Berthaud 1983).

This paper deals with a small leafy lycophyte with diminutive leaves and a stem width not exceeding 2 mm. Because the axes described here are only found as relatively short fragments the material is prone to the interpretative difficulties outlined above regarding its overall size. An argument is put forward suggesting a herbaceous habit. This is based on its consistently narrow stem at all levels of branching and also the presence of acutely curved portions of axis giving rise to terminal strobili. These are interpreted as representing upturned portions of the axis which arose from an otherwise sprawling shoot system.

The lycophyte is preserved as impressions, compressions, and material resembling fusain. The impressions show a range of preservational variation which depended on the effects of compression on the axis and attached leaves, the orientation of the plant in the matrix, and on the extent of sediment accretion around the plant surface, and on the path of the plane of cleavage through the fossil (Thomas and Purdy 1982; Rex and Chaloner 1983; Grierson and Banks 1983; Edwards and Benedetto 1985). The fusain-like material corroborated much of the morphological detail obtained from the impressions and provided additional anatomical and fine morphological information.

## MATERIAL AND METHODS

The locality at Hazel Hill, Puddlebrook is a disused quarry. The fossil plants occur in a laminated but poorly bedded shale with a blue/grey to buff coloration. The quality of preservation is highly variable and much of the material has been badly weathered by the movement of water through the shale. The most common type of

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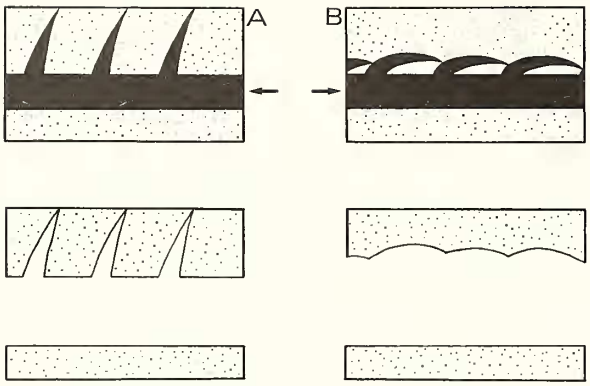


TEXT-FIG. 1. Diagram illustrating the formation of the two principal types of impression surface of *Selaginellites resimus* as seen in hypothetical longitudinal section. A, the microphylls are at a wide angle to the axis at the time of deposition so sediment can penetrate in between the leaves and stem, and form an impression with the surface of the stem. B, the microphylls are at an acute angle to the stem and are actually overlapping and exclude sediment from the spaces between the stem surface and the laminae. In both A and B the organic component of the fossil has disappeared and the plane of cleavage has passed along the middle of the space originally occupied by the stem. The variation between the two types is not brought about so much by the position of the line of cleavage as by the position of the leaves at the time of deposition.

preservation of this lycophyte is as impression material in which organic or compression material is absent. In their study of compressions of *Haskinsia sagittata*, Edwards and Benedetto (1985) draw attention to the fact that plant impressions exist with little or no organic matter in either counterpart. This is certainly the case with the majority of specimens from Puddlebrook. Two well-preserved specimens shown in Plate 10, figs. 1 and 3 illustrate what are probably the two principal configurations seen among the range of material collected, but which both lack organic material. In one, the median microphylls descend into the matrix and are visible as apertures (Pl. 10, fig. 1), but in the other, surface impressions of the median laminae are clearly visible (Pl. 10, fig. 3). In both cases the line of cleavage has passed through the middle of the space originally occupied by the axis (text-fig. 1, arrows). In the absence of any organic matter only impression surfaces remain and the differences between the two forms are believed to result from a difference in the angle of the leaves to the axis and the amount of sediment which accreted in the space between them at the time of deposition. In this way an impression of the stem surface is produced (Pl. 10, fig. 1; text-fig. 1A) because the microphylls were perpendicular to the axis and sediment collected in between, whereas in Plate 10, fig. 3 and text-fig. 1B the median microphylls were at a more acute angle to the stem and effectively sealed off sediment from making contact with the stem surface. Using the terminology of Chaloner and Collinson (1975) and Grierson and Banks (1983) when both counterparts lack organic material these represent a double cleavage impression rather than a cleavage impression united with a cleavage compression. The two configurations displayed here corroborate Rex and Chaloner's (1983) finding that the angle of the leaves to the stem at the time of deposition dramatically controls the appearance of the leafy shoot impression, which is seen here in lycophyte stems of only 2 mm diameter.

Fusainized material is rare and only four specimens with leaves in attachment were found which were consolidated enough to withstand demineralization and observation with the SEM. Because of the close morphological similarity between the three-dimensional impressions and the fusainized axes, both types of

EXPLANATION OF PLATE 10

Figs. 1–3. *Selaginellites resimus* sp. nov. 1, V.62304, impression of axis with dichotomy, three vertical rows of leaves visible. Plane of cleavage has passed through the middle of the space originally occupied by the stem. Median microphyll impressions are visible as flattened letter Ws which descend into the matrix while marginal microphylls are visible as V-shaped grooves, ×4·5. 2, V.62303, branching axis where most of the stem is twisted at 45° relative to cleavage. Left branch is sharply recurved and partially defoliated. In this region are spheroidal depressions (arrowed) which are believed to represent the impressions formed around sporangia. Before the division of the axis the leaves are twisted at 45° to the bedding plane showing alternating arrangement of whole and partially hidden leaves, ×3. 3, V.62305, median microphylls are visible as impressions in surface view instead of descending into the matrix. Note the cordate to deltoid outline, and the attenuated distal tips of the vegetative leaves, ×4.

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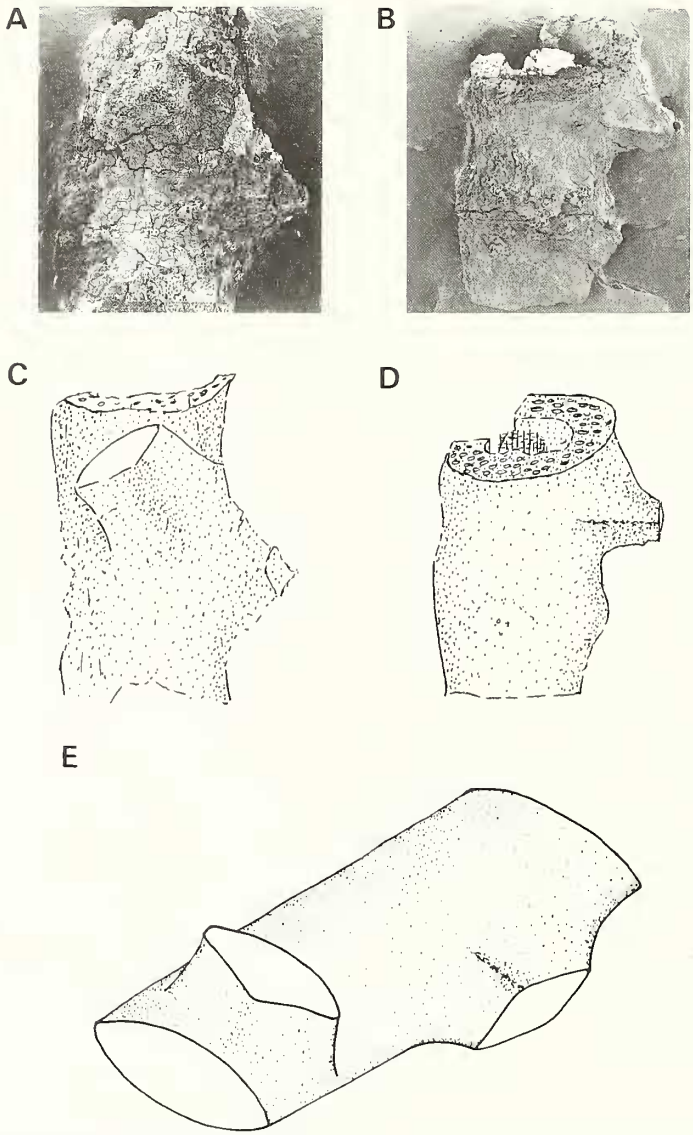
ROWE, *Selaginellites*




TEXT-FIG. 2. *Selaginellites resimus* sp. nov. A, V.62310*a*, fusainized axis with median microphyll in attachment having laminate profile, × 10. B, V.62310*b*, marginal microphyll attached to fusainized axis with evidence of a considerable degree of distortion showing a broad vertical area of attachment, × 10. C, D, line-drawings of V.6231*a* and V.6231*b* respectively, × 10. E, diagram summarizing the effects of compression on an axis of *S. resimus* preserved as fusainized material. Only one median and one marginal microphyll are shown.

preservation are believed to be derived from the same plant species. Although reflectance studies have not been carried out, this material is referred to as fusain merely because of its superficial similarity to fusinite.

In fusainized material the marginal microphylls are often distorted or compressed in a plane perpendicular to the surface of the lamina (text-fig. 2B, D, E). The direction of compression of the flattened microphyll in Plate 12,

fig. 1 is the same as that seen on the axis to which it is attached (Pl. 12, fig. 2). There is a two-fold interest in this observation; first, the difference in susceptibility to compression between the median and marginal microphylls, and secondly, the fact that the material is composed of brittle fusain-like material and yet has been compressed quite substantially without total shattering of the cells visible in the cortex, or the complete breakage of the surface of the marginal microphyll. Text-fig. 2E summarizes the gross morphology of the stem and a median and marginal microphyll after compression. The median microphyll has retained its laminate structure (text-fig. 2A and C), whereas the marginal microphyll is perpendicularly flattened (text-fig. 2B, D; Pl. 12, fig. 1). The behaviour of the median microphylls in *Selaginellites resimus* as seen in the fusainized material, differs considerably to that observed in spines of *Sawdonia ornata* (Chaloner *et al.* 1978) which were observed to have been flattened in a vertical plane, whereas those observed in the fusainized Puddlebrook material were only slightly compressed. This occurred in material which obviously had the potential to be deformed as seen by the distorted marginal microphylls on the same specimen. Unlike the observations on *S. ornata*, where spines on the median surfaces of the axis were distorted (Chaloner *et al.* 1978) it is the marginal leaves which are the most noticeably affected in *Selaginellites resimus*. There is evidence from the impression material that the median leaves, which appear as flattened letter Ws have been partially flattened, but this is in the opposite direction to that observed in the spines on the upper surface of *Sawdonia*. Unfortunately owing to the sometimes highly friable nature of the shale it was not always possible to retain part and counterpart or record the orientation of the fossil in the sediment. Some of the fusainized axes do not show any difference between median and marginal microphylls (Pl. 11, fig. 6). Perhaps an explanation of this is the fact that the shale in which the plant fossils are preserved consists of irregular bands several millimetres thick comprising different sized sediment particles, and it is possible that this affected the compressibility of the matrix surrounding the plant material.

The change in shape of the lateral appendages and the main axis in material that resembles fusain poses some doubt as to its formation and composition. It is inconceivable that brittle and highly fragile structures such as the microphylls and axes of this material could have been distorted and undergone such changes while in this state. Because of the compressed nature of the material, two hypotheses are possible concerning its origin. One is that the conversion to a fusain-like material took place after burial and compression, which would infer that conflagration by wild fire was not responsible for its formation. Alternatively, the organic matter might not represent fusinite *sensu stricto* but consist of some other maceral which preserves anatomical and fine morphological details. The latter explanation may be of some significance when charcoal-like material is observed in the geological record and popularly believed to have originated as a result of conflagration (Alvin 1974; Scott and Collinson 1978; Cope and Chaloner 1980).

The plants were photographed under even or directional lighting. Fusainized material was either wholly or partially removed from the matrix with steel needles and then demineralized in 30% hydrofluoric acid for up to 10 min. Specimens were then washed thoroughly and dried at room temperature. Fusainized specimens were adhered to SEM stubs with silver dag which was applied when semi-dry, so that the fluid did not invade the specimen and ruin any fine detail. Careful application of silver dag and quite prolonged gold coating (up to 6 min) were necessary to reduce charging of this highly fragmentary material when examined by SEM. The specimens and preparations are housed in the Palaeontology Department of the British Museum of Natural History (BMNH, V.62303–V.62330).

The Lower Carboniferous Drybrook Sandstone assemblage at Puddlebrook has been the subject of several papers since Allen (1961) identified the lycophyte sporophyll *Lepidostrobophyllum fimbriatum* from there (Lele and Walton 1962; Thomas 1972; Thomas and Purdy 1982). The material described here was discovered during a recent reinvestigation.

A direct, biostratigraphical age determination of the Puddlebrook assemblage is difficult because of the extreme rarity of animal remains and the poor preservation of miospores (Lele and Walton 1962). The plant-bearing shale outcrops on the western margin of the Wigpool syncline in the northernmost part of the Forest of Dean and is presumed to be continuous with an outcrop of Drybrook Sandstone on the eastern limb of the syncline at Plump Hill. The nearest age determination for the macroflora is based on miospore data collected from Plump Hill (Sullivan 1964). Because of the presence of *Perotriletes tessellatus* and *Schultzospora* (Sullivan 1964) and *Carbaueuletes circularis* (Spinner 1985), an Asbian/Holkerian age or a level equivalent to the TC zone of Clayton *et al.* (1977) is indicated. Correlation of the Puddlebrook locality with that at Plump Hill is substantiated by macrofossil remains of *L. fimbriatum* (Allen 1961) and impressions of fronds resembling *Diplopteridium* Walton, both of which are common elements at Puddlebrook. A poorly preserved spore assemblage from Puddlebrook includes the characteristic palynomorph *Tetrapterites visensis* (Sullivan and Hibbert 1964) which is known from a shale band at the Plump Hill locality and from the Upper Visean of the Carboniferous Limestone in the Menai region of north Wales.

## DESCRIPTION

*Impressions/Compressions.* The axes are 1·5 to 2·0 mm in diameter and up to 7·5 mm wide including the attached leaves. The stems branch isotomously and usually every 2 to 4 cm (Pl. 11, figs. 1–3). In such specimens the diameter of the axis does not change significantly from 2·0 mm over several divisions. The angle of branching ranges between 30° and 80° (Pl. 10, figs. 1 and 2; Pl. 11, figs. 1–3). Three out of the four orthostichies are visible in most specimens (Pl. 10, fig. 3). When the leafy shoots are arranged at 45° to the plane of cleavage a series of alternating, long and short, appendages is seen (Pl. 10, fig. 2). The microphylls are 3·2 to 4·5 mm in length and when seen in surface view are cordate to deltoid in outline and terminate in fine pointed tips (Pl. 10, fig. 3). In some cases the microphylls are not seen in surface view but are visible as slit-like apertures that resemble a flattened letter 'W' (Pl. 10, fig. 1). These apertures are 1·8 mm wide and are sometimes surrounded by a weak ridge or groove. The apertures are interpreted as representing the impressions of leaf laminae which have since weathered away. The microphylls attached to the lateral margins of the stems indicate that the leaves were curved distally. They show a broad, vertical attachment (Pl. 10, fig. 1) which is the same length as the distance between two vertically adjacent leaf bases in the median part of the stem. As was shown above this feature is interpreted as resulting from compression of the marginal laminae which are distorted from an originally laminate aspect.

The terminal parts of some shoots have a different appearance from some of the more proximal parts of leafy axes (Pl. 10, fig. 2, arrow; text-fig. 3A–F), and these are believed to be strobili. Two of the specimens consist of partially defoliated axes with additional circular to oval depressions (Pl. 10, fig. 2; text-fig. 3B, D). A further specimen contains at least eight groups of rounded impressions and these are associated at the bases of closely arranged appendages in the distal portion of the axis (text-fig. 3A). Each depression is 0·9 to 1·8 mm in diameter and is subdivided into several oval or rounded triangular subunits. It is difficult to determine the arrangement and outline of the terminal appendages or sporophylls on this specimen as they lack the pointed distal tips characteristic of the more proximal leaves. This specimen represents an impression of a small terminal, compact strobilus, with the depressions representing the rounded impression surfaces of the sporangia at the sporophyll bases. This suggestion is supported by the specimen illustrated in text-fig. 3B–F. The specimen is complicated by the fact that two separate branches arise from the bend in the vegetative stem. The branch to the right side is attached to the proximal vegetative axis, and it is possible that the additional branchlet is either superimposed or represents part of a dichotomizing fertile region. Unlike the specimen in text-fig. 3A, many of the sporophylls have been shed but two or three are still attached to the slender axis and are visible in surface view (text-fig. 3C, E). The sporophyll is not pointed distally, and in addition to this, there is at least one circular impression of a megaspore which is flattened against the surface of the cordate sporophyll (text-fig. 3E, F). To the outside of this (arrow) there is a raised ridge of sediment which formed the impression surface around the megasporangium which is 1·6 mm in diameter. The uppermost surface is broken and reveals four empty spheroidal areas (text-fig. 3E, F) each of which is equivalent in size to the mineral cast of the megaspore, immediately above. This complex is interpreted as representing a tetrad of megaspores which formed a three-dimensional impression from which the organic matter has since disappeared. The minute mineral impression surfaces visible in these areas are complex and were presumably formed by mineral (Spicer 1977) or very fine sediment accretion around and inside the sporangium which even formed an impression surface of the presumably spiny megaspores. A very similar type of small-scale impression surface is seen around megaspores of *L. fimbriatum* from the same locality (Allen 1961).

*Fusainized material.* One specimen, although having little fine structure preserved, shows sufficient gross morphology to compare very closely with the impressions described above (Pl. 11, fig. 6). There is clearly little evidence to suggest any development of a leaf cushion or expanded leaf base. Instead the microphylls emerge from the axis as simple laminate structures. Although there was generally no cellular detail of the stem surface (Pl. 11, figs. 4 and 6), in one specimen the structure of the cortex and the xylem was preserved. The cortex is between 250

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EXPLANATION OF PLATE 11

Figs. 1–7. *Selaginellites resimus* sp. nov. 1, V.62311; 2, V.62306; 3, V.62312; all ×0·75. Note equal dichotomies and the maintenance of a consistently narrow stem diameter at all levels of branching. 4 and 5, V.62310, oblique view of fusainized microphyll base with lens-shaped profile attached to main axis, ×30. 5, abaxial surface of microphyll close to junction with axis. Note the irregular surface with raised stomata (left) and the fractured surface, representing the hypodermal layer (right), ×200. 6, V.62309, fragment of fusainized vegetative axis with laminate, deltoid to cordate leaves arranged in four vertical rows, ×14. 7, V.62310, group of stomata on abaxial surface of leaf with conspicuous rim or ridge perched above guard cells, ×550.

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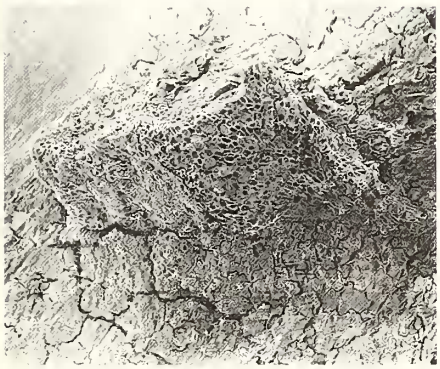

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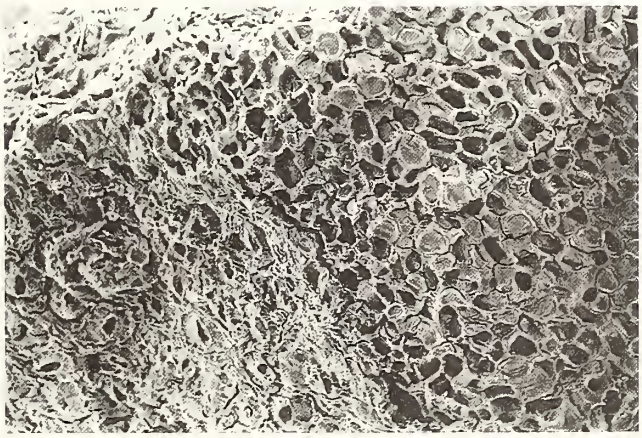

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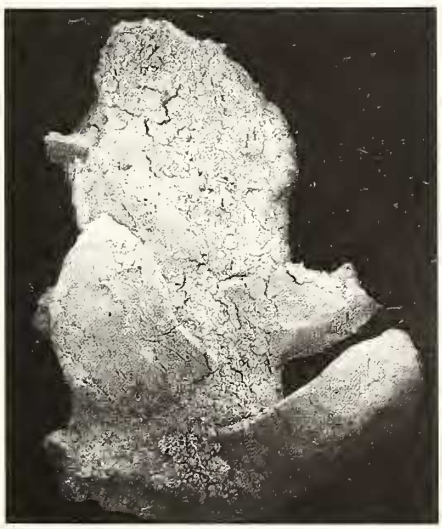

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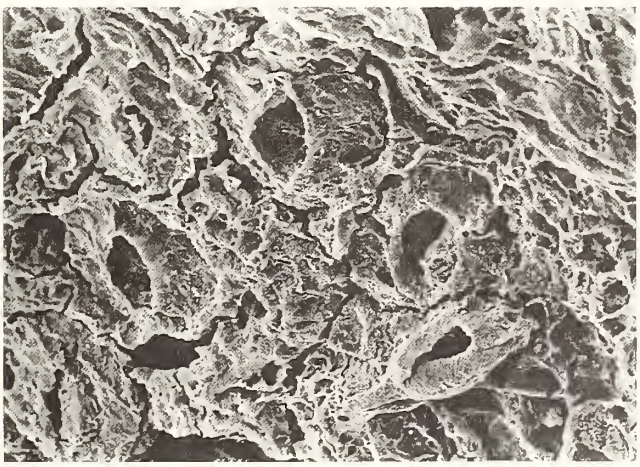

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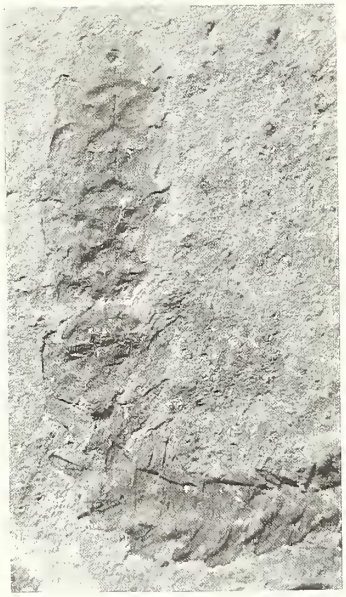

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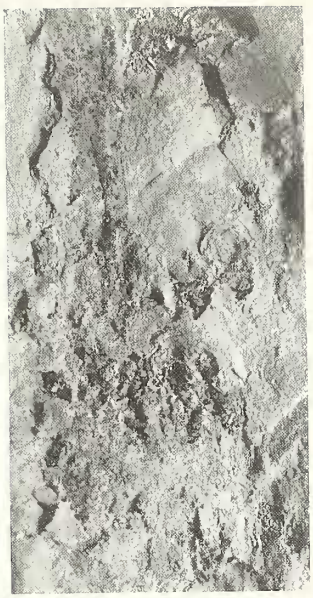

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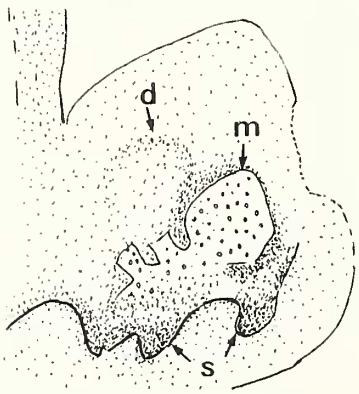


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to 350 μm wide, and encloses the xylem which is 400 μm in diameter (Pl. 12, fig. 2). The cortical cells are oval to isodiametric in transverse view and 15 to 45 μm in diameter. There is little differentiation of the cortex into zones except a tendency for the smaller elements to be at the outside. The vascular tissue is rarely preserved and only fragmentary remnants of the tracheids are normally visible as oblique, transverse, and longitudinal fracture surfaces (Pl. 12, figs. 3–5). The xylem is separated from the cortex by a narrow space. It is 400 μm in diameter and composed of scalariform tracheids (Pl. 12, fig. 3). The tracheids apparently decrease in width from the inner to the outer part of the stele and range from 19 to 25 μm in diameter. The protoxylem is therefore probably exarch. The xylem is not sufficiently well preserved to determine whether protoxylem points were present, but the arrangement of some of the smaller protoxylem elements suggest this (Pl. 12, fig. 3). The tracheids are at least 60 μm long and possess scalariform ridges which are 3 μm thick. The wall material between the scalariform bars consists of a membraneous layer comprising four or five circular to oval pits which are approximately 1 to 2 μm in diameter and apparently confined to the tangential walls of the tracheids (Pl. 12, figs. 4 and 5). It is not known whether these different layers represent secondary wall development or both primary and secondary layers. High magnification of transversely fractured cell walls indicate that the thin, pitted wall layer appears as a series of broken pegs attached to a layer of wall material which is continuous with the thick, adjacent scalariform bar (Pl. 12, fig. 4). The cell walls of adjacent tracheids are sometimes separated by a narrow groove (Pl. 12, fig. 4, arrow). It is possible that this might represent the position of the middle lamella.

Only one fusainized microphyll provided any evidence of a structure resembling a ligule or ligule pit but this is by no means certain (Pl. 12, fig. 1, arrow B). Stomata are present on the abaxial surface of the leaves and have a frequency of 340 to 370 per $mm^2$ (Pl. 11, figs. 5 and 7). Of four specimens with cellular details, three 'types' of stomata were identified which are believed to represent preservational variations of the same structure (text-fig. 4). The stomata are 35 to 38 μm long and 28 to 38 μm wide. In one specimen (text-fig. 4A) both guard cells are clearly visible, although the surrounding organic material is not well preserved. There is a broad stomatal aperture and an irregular ridge is present on the outer surface of both guard cells. In another specimen (text-fig. 4B), the stomata have a different appearance. There is a rim or ridge on the outer surface of the guard cells and just inside this are the inner faces of the guard cells which line the stomatal aperture. The best preserved type of stoma (text-fig. 4C) comprises a pair of guard cells which is raised above the surface of the leaf and partially overlain by a skirt of organic material which might represent cuticle. The stomata are closely arranged and are separated by narrow grooves which might indicate the position of modified subsidiary cells. Part of the abaxial surface of one microphyll shows details of the hypodermis (Pl. 11, figs. 4 and 5). On the right part of the leaf the outer surface layer of disorganized organic material has broken away to reveal a thick-walled hypodermis of randomly arranged, isodiametric to oval cells, 15 to 34 μm in diameter. The upper epidermis of the microphyll, as seen on a laterally distorted microphyll, consists of elongate cells that are aligned with the long axis of the microphyll (Pl. 12, fig. 1). The cells that are close to the central ridge are irregular in outline and approximately 20 to 28 μm in diameter.

A transverse fracture through the base of a microphyll seen on one specimen (Pl. 12, fig. 6) shows several zones

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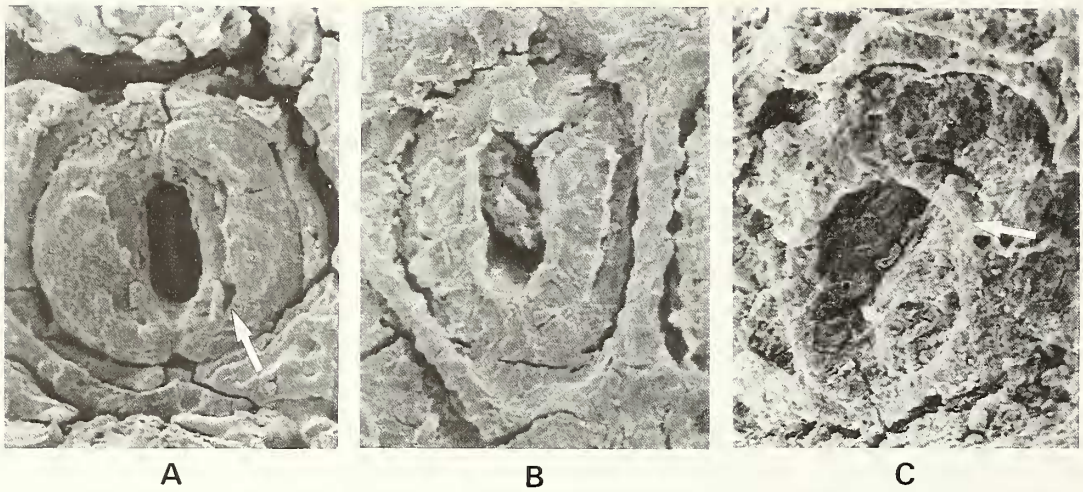
TEXT-FIG. 3. *Selaginellites resimus* sp. nov. A, V.62307, a vegetative axis is sharply curved and gives rise to a small compact strobilus. The sporophylls lack the attenuated distal tips characteristic of the vegetative leaves. Groups of spherical depressions along a central position of the strobilus represent the impressions of sporangia, × 4. B–F, V.62308, holotype. B, curved axis giving rise to one, possibly two, strobilar axes. The upper branch shows evidence of a blunt, cordate sporophyll associated with a complex, three-dimensional impression surface of a megaspore tetrad (arrowed), × 3·5. C, enlargement of area of strobilus arrowed in B. The broad sporophyll differs considerably from the vegetative leaves and is partially superimposed at its base by the complex impression surface of a megaspore tetrad, × 10. D, line-drawing of holotype showing arrangement and position of fertile areas in relation to vegetative part of axis, × 4·5. E, enlargement of sporophyll and megaspore tetrad impressions. The lower part of the tetrad impression consists of a mineral layer which covered the outer part of the sporangium and megaspores. Immediately above is a roughly circular impression surface with minute apertures which is interpreted as representing an impression surface of a spiny megaspore. Immediately to the left of this structure is an oval depression also assumed to represent the impression or indentation in the matrix of a megaspore, × 18. F, line-drawing of features seen in E, the megaspore impression (m), the depression in the matrix formed by a megaspore (d), and the cavity once containing megaspores and partially overlain by a thin wall of mineral matter (s), × 18.

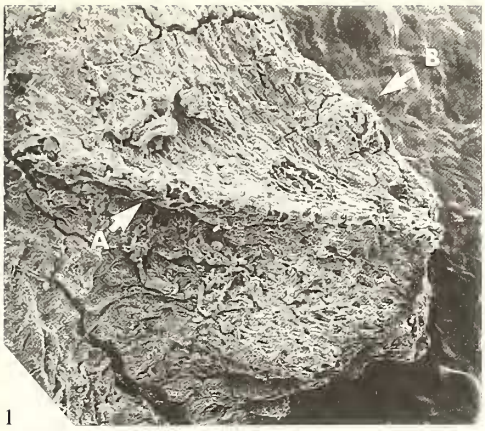



TEXT-FIG. 4. Preservational variation of stomatal complexes in fusainized *Selaginellites resimus* sp. nov. A, V.62315, the pair of guard cells has a flattened profile and is sunk below the surface of the microphyll. An outer layer of material covers each guard cell which has an irregular inner edge (arrowed) surrounding the stomatal aperture, × 1400. B, V.62309, the stomatal complex is sunk below the surface of the leaf but the guard cells are not clearly visible. There is an oval hoop of material which terminates as a well-developed rim above the stomatal aperture, × 1400. C, V.62310, the stoma is raised above the level of the leaf surface and consists of two guard cells which are contained beneath a skirt of material terminating in a rim (arrowed) above the stomatal aperture, × 1800.

of cells. The hypodermis is two cells thick near the edges of the lamina and three to four cells deep closer to the midrib. The xylem consists of a single strand of about thirty tracheids (Pl. 12, fig. 8), 8–15 μm in diameter. They possess scalariform to reticulate thickenings (Pl. 12, fig. 7). In transverse section a series of peg-like outgrowths indicates that the tracheid wall was thin and pitted between the scalariform bars (Pl. 12, fig. 7). The vascular strand of the leaf is 250 μm in width. Immediately adaxial to the xylem, a number of thin-walled elements are visible which are arranged perpendicularly to the lamina (Pl. 12, fig. 6). Each element is about 75 μm long and 20 μm wide. This is interpreted as a zone of palisade parenchyma in the adaxial half of the microphyll.

## EXPLANATION OF PLATE 12

Figs. 1–8. *Selaginellites resimus* sp. nov. 1–5, V.62310*b*. 1, marginal microphyll showing evidence of compression in a direction perpendicular to the plane of the leaf resulting in the formation of an apparently broad vertical area of attachment to the axis. A transverse ridge (arrow A) indicates the original position of the lamina margin and this corresponds well with the impressions of lateral microphylls. A structure on the folded adaxial surface may represent a ligule pit (arrow B), × 45. 2, transverse fracture of axis showing the position of the cortex and xylem. Although the whole structure has been compressed the cortex is relatively complete and uncrushed, × 40. 3, transverse fracture surface of tracheids from main axis showing distribution of protoxylem elements towards the outer part of the xylem (lower right), × 500. 4, oblique view of tracheid of main xylem. The fractured part of the cell wall between the scalariform bars consists of a number of small pegs (arrow), × 2000. 5, longitudinal fracture surface of tracheid from main xylem with angular scalariform bars with thin pitted walls in between, × 1500. 6–8, V.62310*a*. 6, transverse fracture surface of base of attached microphyll showing a layer of elongated palisade parenchyma above the leaf trace, × 220. 7, tracheids of leaf trace with scalariform to spiral thickenings of the cell wall, × 900. 8, leaf trace of attached microphyll consisting of approximately 30 tracheids, × 350.




1

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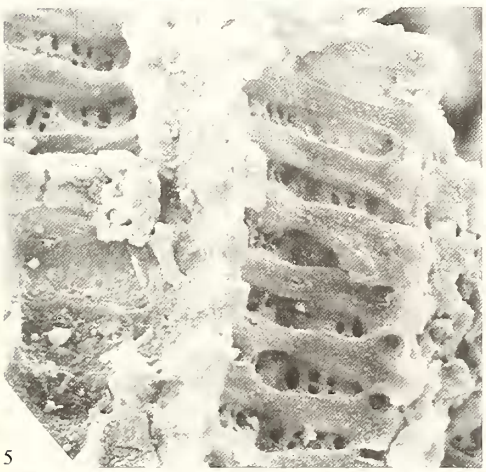

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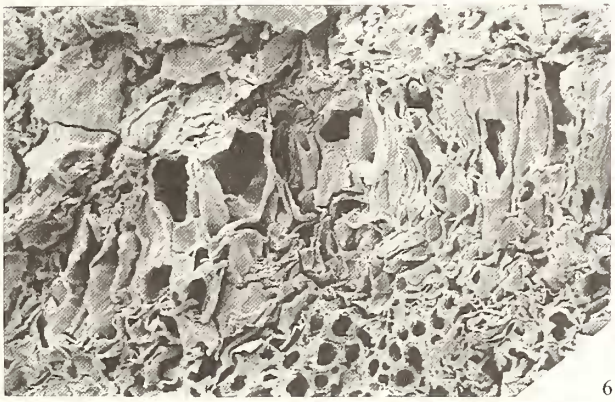

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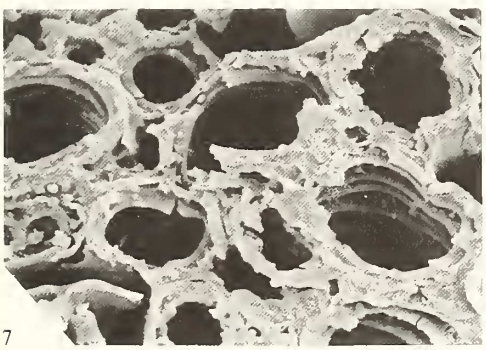
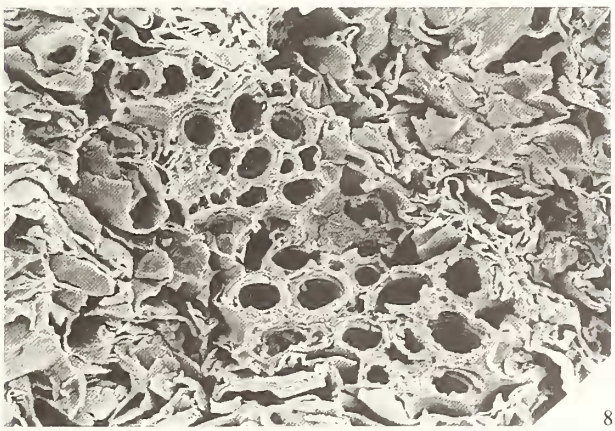


7



8

ROWE, *Selaginellites*

## SYSTEMATIC PALAEONTOLOGY

Class LYCOPSIDA
Order SELAGINELLALES
Family SELAGINELLACEAE
Genus SELAGINELLITES Zeiller (1906)

*Type species. Selaginellites suissei* Zeiller (1906), Stephanian of Blanzy, France.

### *Selaginellites resimus* sp. nov.

Plate 10, figs. 1–3; Plate 11, figs. 1–7; Plate 12, figs. 1–8; text-fig. 1A and B; text-fig. 2A–E; text-fig. 3A–F; text-fig. 4A–C

*Derivation of name.* Latin *resimus*, bent backwards or upwards, referring to the upturned portion of the axis containing the strobilus.

*Holotype.* V.62308, text-fig. 4B–F.

*Locality.* Hazel Hill quarry, Puddlebrook, near Drybrook, Forest of Dean, Gloucestershire, Great Britain.

*Horizon.* Shale band in the Drybrook Sandstone formation, Lower Carboniferous (Asbian–Holkerian).

*Diagnosis.* Leafy shoots at least 5 cm long, 1·5–2·0 mm in diameter, remaining narrow at all levels of branching. Microphylls deltoid with attenuated distal tips, 3·2–4·5 mm long and 1·8–2·0 mm wide, broadest at a point a third of the distance from the base, and arranged in four vertical orthostichies with a strict opposite and decussate arrangement. Stomata 35–38 $\mu$m long and 28–38 $\mu$m wide, frequency 340–380 per mm$^2$. Stomatal aperture 16 $\mu$m long by 6–8 $\mu$m wide. Cortex 250–350 $\mu$m thick. Xylem exarch, 400 $\mu$m in diameter. Walls of tracheids with scalariform thickenings and thin aperturate primary wall. Tracheids up to 25 $\mu$m in diameter and at least 60 $\mu$m long. Leaf lamina 0·5 mm thick at base with adaxial palisade parenchyma, 80 $\mu$m thick. Hypodermis 2–4 cells thick. Xylem exarch, 250 $\mu$m in diameter. Hypodermis, 2–4 cells thick. Strobilus 15–17 mm long and 5 mm wide, consisting of cordate sporophylls with blunt tips. Megasporangia 1·6 mm in diameter. Megaspores with minute spines.

*Comparisons.* The axes from Puddlebrook show some resemblance to the leafy shoots described by Lacey (1962) as *Clwydia decussata* from the Lower Brown Limestone of North Wales, particularly in the decussate arrangement of the leaves in four vertical rows. However, *S. resimus* is smaller and its leaves are only 3·2–4·5 mm in length whereas those of *C. decussata* are up to 12 mm long. Another difference lies in the nature of leaf attachment. In *S. resimus* the leaves are laminate at their attachment with the stem but in *C. decussata* they are reported as cone-shaped at the base (Lacey 1962). Fairon-Demaret and Banks (1978) also interpret a similar cone-shaped base from marginal microphylls of *Archaeosigillaria vanuxemi*. As shown above in the comparison of median and marginal microphylls and their behaviour during compression, it is necessary to interpret the point of leaf attachment with care when attempting to reconstruct the original three-dimensional structure of the stem and the exact mode of attachment of the leaves.

Another record of a *Clwydia*-like plant is from the Arundian or Holkerian, Ravonstonedale, Cumbria (Nudds and Taylor 1978). The material is fragmentary and comprises consistently narrow axes with four vertical rows of decussate leaves, preserved as calcite and sediment infills in a hard brown limestone. Although only the gross morphology is preserved it is closer in size to *S. resimus* than *C. decussata*. The microphylls have attenuated tips, and, if this unusual type of preservation has retained the gross morphology of the leaves, they are very similar to the Puddlebrook microphylls in having a flat profile rather than a conical leaf base. Nudds and Taylor interpret some of the axes as fertile areas, on account of an alternating series of long and short appendages. However, Lacey (1962) pointed out that such a configuration was seen in *C. decussata* as a result of the stem simply being twisted about 45° and this would also seem to be the case among the vegetative axes described here and from Cumbria.

Leafy shoots which are comparable to *S. resimus* include some leafy axes from the Calciferous Sandstone series, Shap Toll bar, Cumbria. These were first described by Kidston (1885) and named *Lycopodites vanuxemi*. The material consists of seven pieces of a hard siltstone containing isolated fragments of leafy shoots of which two show some degree of branching. These were illustrated by Chaloner (1967). Kidston (1901) included all this material in his genus *Archaeosigillaria*. He also included a lycophyte axis from the Upper Devonian of New York

State figured by Vanuxem (1842). This species consists of stems up to 25 mm in diameter with hexagonal to oval leaf base areas in a spiral arrangement on the stem. Kräusel and Weyland (1949) separated all of Kidston's Cumbrian material from the American *A. vanuxemii* and renamed it *A. kidstoni*. This approach has since been followed by Crookall (1966), Chaloner (1967), and Nudds and Taylor (1978). Lacey (1962) was the first to point out the possibility that two types of lycophyte axis were present in Kidston's material. One consisting of narrow shoots with decussate leaves, he guardedly suggested as conspecific with his *C. decussata* from North Wales, and the other comprised broader axes with irregular oval to hexagonal areas in a spiral and/or vertical arrangement on the stem. In deciding whether two types of axis are present in the Shap Toll bar material, the crux of the matter is whether two of Kidston's specimens (Chaloner 1967, fig. 340C, D) really show a connection of broader axes with the type of narrow decussate shoot present as isolated axes in the same material (Chaloner 1967, fig. 340A), and those identified as *Clwydia* from North Wales. After reinvestigating Kidston's material it became clear to me that the material is just not sufficiently well preserved, and there are too few specimens to determine accurately the critical morphological features of both types of axis. Some of the axes from Cumberland have crossing parastichies and vertical orthostichies with slender, oval to fusiform areas demarcated by thin bands of black coaly matter. It is extremely difficult to determine whether these areas represent leaf bases or the remains of resistant fibre-like tissue within the stem. Unless these areas can be shown to represent critical structures such as the outline of a raised leaf cushion or a decurrent leaf base, it is highly questionable as to whether they can be equated with the hexagonal areas visible on the shoots of *C. decussata* (Lacey 1962, text-fig. 12B, C, E). Only one specimen from Cumbria (Chaloner 1967, fig. 340A) has the same type of leaf and leaf arrangement as *C. decussata* and *S. resimus* and this is not attached to a broader axis. The narrower axes which terminate the broader stems in Kidston's material have poorly preserved leaves which are not visible in surface view and it is not possible to compare them critically. Lacey distinguished *C. decussata* from *Lycopodites* Lindley and Hutton by its strictly opposite and decussate leaf arrangement and its cone-shaped leaf bases. Following Lacey (1962) and Grierson and Banks (1963), the broad axes from Cumbria with irregular, hexagonal to fusiform areas on the stem are referred to as *A. kidstonii*. This is mindful of the fact that the material needs reinvestigation particularly with regard to its relationship to the American *A. vanuxemi* and other Lower Carboniferous lycophyte compressions such as *Eskdalia* Kidston. Isolated slender axes not exceeding 2–3 mm in width, with decussate leaves having cone-shaped bases should be referred to as *Clwydia*.

The stomata observed in fusainized specimens of *S. resimus* exhibit considerable variation in structure. All three stomatal types possess a rim or ridge which occurs on the outer surface of the guard cells or a layer of cuticle on their outer surface. The superficial nature of the guard cells, observed in what is believed to represent the best preserved material, differ considerably to the sunken guard cells characteristic of the lepidodendralean stomata (Thomas 1974), but show a remarkable resemblance to those of *Lycopodium clavatum* L. illustrated by Thomas and Masarati (1982) particularly with regard to the raised guard cells and the presence of a ridge or rim around the stomatal aperture.

The anatomy of a number of herbaceous lycophytes is known from the Middle Devonian to the Lower Carboniferous and the wall structure of the tracheids is remarkably uniform. Many consist of exarch protosteles with numerous, often more than ten, protoxylem points (Alvin 1965; Phillips and Leisman 1966; Banks *et al.* 1972; Fairon-Demaret 1977; Grierson and Banks 1983). The structure of the metaxylem elements in *S. resimus* is similar to that in *Barsostrobus* Fairon-Demaret (1977). Both have scalariform thickenings which are 2–4 $\mu$m thick and thin pitted walls in between. Fairon-Demaret (1977) pointed out that two quite different images were seen from conventional light micrographs and SEM pictures of the tracheid wall. The scalariform bars were thread-like when observed with the light microscope but more robust when viewed with the SEM. This is a major problem when attempting to compare anatomy.

Reports of truly herbaceous *Selaginella*-like axes are relatively rare in Carboniferous assemblages. Because of the vegetative similarity between members of the Lycopodiales and Selaginellales among extant forms there is some difficulty in assigning fossil vegetative remains to one or other of these groups as both may contain isophyllous and anisophyllous forms with leaves arranged in spirals or vertical ranks. The generic assignment of the Drybrook axes follows Chaloner (1967) whereby axes showing evidence of heterospory are assigned to the genus *Selaginellites*. Among the Carboniferous species of *Selaginellites* the type species *S. suissei* is approximately the same size but it has anisophyllous leaves which are, however, arranged in four vertical ranks. The leaf margins are fimbriate which also distinguish it from *S. resimus*. It is interesting that the specimen described by Kidston (1901) from the Westphalian B of Yorkshire consists of a fertile axis divided into two equal parts which might be the case in one of the specimens described here.

*Size and habit*. It is thus possible that the leafy shoots described here belonged to a small, truly herbaceous or epiphytic lycophyte with persistent decussate leaves and small terminal strobili. A herbaceous habit is most likely

because the stems do not exceed a width of 2 mm. In addition to this, a number of specimens show a distinct curvature of the axis occurring shortly before the terminal fertile parts of plant. While it is arguable that these axes have been bent during transport or burial, the number of occasions that the feature was observed below the terminal parts of shoots more compellingly suggests that the axes were curved in life. Grierson and Banks (1983) envisage *Haskinsia* as being a herbaceous lycophyte with 'a trailing stem and ascending dichotomising axes'. I consider that the curved axes of *S. resimus* provide evidence of this type of habit. A similar sprawling growth was suggested for *Paurodendron fraipontii* (Schankler and Leisman 1969) which is also consistent with many extant species of *Selaginella.*

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